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Climatic water availability is the main limiting factor of biotic attributes across large-scale elevational gradients in tropical forests ☆

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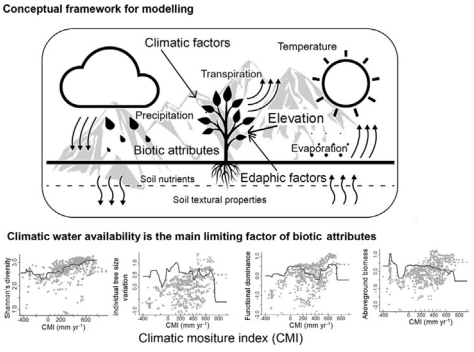
HIGHLIGHTS

- Climatic water availability was a main spatial driver of biotic factors.
- Taxonomic diversity increased with climatic water availability.
- Biotic factors increased monotonically with soil fertility but decreased with soil pH.
- Tree size or biomass-related biotic attributes are sensitive to future drought and heat.

GRAPHICAL ABSTRACT



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ABSTRACT

Climatic water availability is a key spatial driver of species distribution patterns in natural forests. Yet, we do not fully understand the importance of climatic water availability relative to temperature, and climate relative to edaphic factors for multiple biotic attributes across large-scale elevational gradients in natural forests. Here, we modelled multiple abiotic factors (elevation, climate, and edaphic factors) with each of the taxonomic-related (Shannon's species diversity, species richness, species evenness, and Simpson's dominance) and tree size or biomass-related (individual tree size variation, functional dominance and divergence, and aboveground biomass) biotic attributes through boosted regression trees (BRT) models, using biophysical data from 247,691 trees across 907 plots in tropical forests in Hainan Island of Southern China. The tested multiple abiotic factors explained simultaneously 43, 50, 36, 45, 37, 50, 17 and 46%, respectively, of the variations in Shannon's species diversity, species richness, species evenness, Simpson's dominance, individual tree size variation, functional dominance, functional divergence and aboveground biomass. After the large influences of elevation (i.e. 30.43 to 62.83%), climatic water availability accounted for most (i.e. 15.52 to 25.30%) of the variations in all biotic attributes. Beside the increasing trend with elevational gradients, taxonomic diversity increased strongly with climatic water availability whereas tree size or biomass-related biotic attributes showed strong decreasing and increasing trends. Tree size or biomass-related rather than taxonomic-related biotic attributes also decreased apparently with mean annual temperature. Most of the biotic attributes monotonically increased with soil fertility but decreased with soil pH, whereas soil textural properties had mostly negligible influences. This study strongly reveals that future climate change (i.e. a decrease in climatic water availability with an increase in mean annual temperature) is thus likely to have a substantial influence on the biotic attributes in the studied tropical forests across large-scale elevational gradients.

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1. Introduction

Topography (e.g. elevational gradients) is a key spatial driver of plant biodiversity, composition, stand structural complexity and aboveground biomass in tropical forests, as it constrains micro- and macroclimatic conditions, soil nutrients and hydraulic conditions within which trees grow (Jucker et al., 2018). However, it is generally well-accepted that biotic attributes (e.g. plant biodiversity, composition, stand structural complexity and aboveground biomass) are limited by three key abiotic factors, such as climatic water, energy (i.e. either solar radiation or temperature) and soil nutrient availability, across large-scale geographical gradients (Gillman et al., 2015; Poorter et al., 2017). Yet, across the globe, there is little understanding about the relative importance or contribution of multiple abiotic drivers for multiple biotic attributes in natural forests. Specifically, the importance of climate relative to edaphic factors for multiple biotic attributes remains unclear in natural forests across large-scale elevational gradients.

Across a wide range of biogeographical gradients, climate (i.e. mean annual temperature and water availability) and edaphic (i.e. soil physicochemical properties and texture contents) factors can largely influence biotic attributes through variations in metabolic kinetics, physiological and environmental determinants of plant growth (Anderson et al., 2006; Chu et al., 2016; Michaletz et al., 2018; Paquette and Messier, 2011; Poorter et al., 2017). For example, the rates of photosynthesis and respiration exponentially increase with favorable ranges of temperature (i.e. available energy) to a critical value (i.e. high temperature, and hence heat) beyond which rates including net primary productivity decrease (Berry and Bjorkman, 1980; Ciais et al., 2005; Michaletz et al., 2014). More specifically, increasing temperatures (i.e. heat) may imply lower tree growth in tropical forests because temperatures are already high in tropical forests (Clark et al., 2003). As such, it is also well-understood that most of the tree species (i.e. about 72%) are sensitive to temperature variation, and even to a very small range in temperatures (e.g. 24 to 27 °C), in tropical forests (Toledo et al., 2012). In addition, climatic water availability and drought sensitivity are recognized as main influencing factors for the species distribution, diversity and ecosystem functioning in tropical natural forests (Bongers et al., 1999; Poorter et al., 2017; Toledo et al., 2012). For example, high precipitation (and thus high climatic water availability) increases the length of the growing season, which in turn increases the plant growth, survival and recruitment, and hence higher aboveground biomass or productivity at stand level (Poorter et al., 2017; Toledo et al., 2012). As such, but in the opposite way, several theories related to climate change scenarios predict and empirical studies suggest that droughts (i.e. low climatic water availability) may lead to increased tree mortality and hence reduced aboveground biomass in both short-term (Phillips et al., 2010) and long-term (Poorter et al., 2017). However, small mismatches between the theories and empirical studies still exist in the literature, probably due to the differences between experimental and natural studies. For example, climatic water availability increases the annual biomass growth and survival rates, whereas high temperature decreases biomass growth but high precipitation events also increase mortality rates in tropical natural forests (Aubry-Kientz et al., 2015; Clark et al., 2003; Poorter et al., 2017). Yet, the importance of climatic water availability relative to mean annual temperature for multiple biotic attributes is less consensual across large-scale elevational gradients in natural forests.

It is generally well-understood that climatic factors relative to edaphic factors explain higher variations in species distribution patterns, biodiversity and ecosystem functioning in natural forests (Poorter et al., 2017; Toledo et al., 2012). The highest importance of climate relative to edaphic factors is probably due to the fact that climatic factors vary over large-scales whereas edaphic factors vary at small-scales, and hence edaphic factors act as an additional ecological filter for influencing biotic attributes at local- and small-scale environmental conditions (Swaine, 1996; Toledo et al., 2012). For example, it has been increasingly reported that high aboveground biomass or productivity is often located on nutrient-poor soils in subtropical and tropical forests at local- and small-scales (Ali and Yan, 2017; Chiang et al., 2016; Malhi, 2012; Prado-Junior et al., 2016; Singh et al., 1989; Singh et al., 2017), and hence contrary to the predictions of the soil fertility hypothesis (Quesada et al., 2012; Wright et al., 2011). Indeed, soils can be very variable in their types and textural properties, and hence may also influence the soil nutrients, and water flow and availability to the plants (Sala et al., 1988; Sanaei et al., 2018; Toledo et al., 2012). However, many hypothesized mechanisms regarding the influences of multiple edaphic factors on multiple biotic attributes in natural complex forests remain empirically untested (Michaletz et al., 2018; Poorter et al., 2017). For example, the inverse-texture hypothesis suggests that high productivity is located on fine-textured and wet soils in humid regions while located on coarse-textured soils in arid regions following a reduction in evaporation (Noy-Meir, 1973; Sala et al., 1988). Surprisingly, this hypothesis has received much less attention in complex natural forests as compared to the grasslands and rangelands (Lane et al., 1998; Sanaei et al., 2018). Moreover, little is known about the influence of multiple edaphic factors relative to climatic factors on multiple biotic attributes across global forest ecosystems.

Tropical forests are most structurally complex and important carbon sinks in the terrestrial ecosystems as they could sequester and process a large amount of carbon through photosynthesis and respiration mechanisms (Malhi, 2012; Pan et al., 2011). Therefore, identifying the main limiting factor of biotic attributes is urgently needed for the conservation and enhancement of these carbon sinks within a specific region across different forest types and biomes (Durán et al., 2015; Jucker et al., 2018; Poorter et al., 2017). Accordingly, in this study, we aim to evaluate how multiple biotic attributes (e.g. taxonomic- and tree size or biomass-related indices) are related to multiple abiotic drivers (climate and edaphic factors) across large-scale elevational gradients in tropical forests. Specifically, we address the following two major questions, using biophysical data from 247,691 trees across 907 plots in tropical forests in Hainan Island of Southern China. First, what are the relative contributions of multiple abiotic drivers for biotic attributes in tropical forests? Second, what is the main limiting factor (in terms of both relative contribution and influence) of biotic attributes along large-scale elevational gradients in tropical forests? We hypothesize that biotic attributes are strongly influenced by climatic water availability along large-scale elevational gradients because climatic water availability has been shown to influence species distributions, survival and recruitment rates more than edaphic factors in tropical forests (Poorter et al., 2017; Swaine, 1996; Toledo et al., 2012). Our proposed hypothesis leads to two main predictions: 1) taxonomic diversity-related biotic attributes, including Shannon's species diversity, species richness, evenness and Simpson's dominance, may increase with increasing climatic water availability along large-scale elevational gradients, probably due to the stronger response of species coexistence and distributions to climate as compared to edaphic factors because of the hierarchy in environmental filters (Swaine, 1996; Toledo et al., 2012); and 2) tree size or biomass-related biotic attributes, including individual tree size variation, aboveground biomass, and functional dominance and divergence, may show unclear or unpredictable trends with increasing climatic water availability along large-scale elevational gradients, because plant species differ in their tolerance of and requirements from the environment probably due to the fact that different sized trees may have different consequences on biomass demographic processes and also different habitat requirements for water and soil nutrients within a given community (Poorter et al., 2017; Swaine, 1996; Toledo et al., 2012). This study may serve as a tool for predicting plant biodiversity and ecosystem functioning based on climatic factors and edaphic factors along large-scale elevational gradients in natural forests.

2. Materials and methods

2.1. Study area and forest inventory data

This study was conducted on Hainan Island (latitude 18°10 -20°10 N, longitude 108°37′-111°03′E) in Southern China. Hainan Island covers

33,900 km^2 of the land area and located at the northern edge of the tropics. A tropical monsoon climate characterizes the area includes distinct dry and wet seasons including typhoons. The main zonal vegetation is characterized as a tropical rainforest and tropical monsoon forest. In this study, we used data from 907 plots distributed across the Hainan Island of Southern China (Fig. S1). Across studied plots, mean annual precipitation ranged from 1008 to 2038 mm, mean annual temperature from 17 to 25 °C, mean annual potential evapotranspiration from 1125 to 1451 mm, elevation from 1 to 1819 m.a.s.l., and the soil total exchangeable bases from 2.2 to 28.5 cmol kg^{-1}. The soils are classified as Acrisols, Arenosols, Alisols, Andosols, Anthrosols, Cambisols, Fluvisols, Ferralsols, Leptosols, Regosols, Nitisols, and Solonchaks in the Harmonized World Soil Database (FAO et al., 2012).

Prior to 1950s, the area occupied by forests on Hainan Island was largely natural, whereas the non-forested area was mainly farmland. In the history, forest area had been subjected to both anthropogenic and natural disturbances, and hence decreased considerably due to logging for timber, windthrow through typhoons, artificial plantations, and residential expansion, with natural forest cover reached to a minimum level in the 1980s. In response to this dramatic loss of the natural forest cover due to the variable intensities of the human disturbances, the Hainan Provincial Government implemented logging ban rules in the natural forests in 1994. The secondary forests in the region have been protected from anthropogenic activities for the last 25 years or more, whereas the old growth forests have been protected from complete clearance for centuries. Consequently, the studied region contained both secondary and old growth forests. We selected forest stands that had recovered naturally from logging in the study region including old growth forests, with no visible anthropogenic disturbances for more than four decades (Lin et al., 2017). Therefore, the areas of our studied 907 plots ranged from 0.035 to 0.25 ha where most of the plots were square and few of them were almost rectangular in shape. The size of the plot depends on several factors such as physical constraints in the studied area, historical anthropogenic disturbances, community structure and the abundance of big trees etc.

In this study, we used biophysical data from 907 plots distributed randomly across the Hainan Island of Southern China (Fig. S1). In each plot, during April 2009–August 2017, all individual trees having a diameter at breast height (DBH) ≥ 3 cm were separately measured and recognized to species-level, and the total tree height for each tree was also measured. For the identification of species in Latin names, Chinese Flora Database (http://foc.eflora.cn/) was used. It is important to mention here that most of the species were identified to their Chinese names in the field, and then Chinese Flora Database was used to assign the Latin names to the identified species. The unidentified species in the field were brought back to the nearest Forest Research Station for identification through the help of taxonomists or local experts. As recommended by previous methodological and empirical studies for biodiversity and ecosystem functioning (Conti and Díaz, 2013; Cornelissen et al., 2003; Pakeman and Quested, 2007), we covered and identified 75% to 95% of the most of the abundant and dominant species of the total community (i.e. plot) coverage across 907 forest plots, based on both the species' relative frequency and relative basal area within each plot. This forest inventory resulted in a total of 247,691 individuals belonging to 994 identified species, 378 genera and 104 families across 907 plots (see Appendix A for a summary of studied species).

2.2. Response variables: Biotic attributes

In this study, we used eight biotic attributes as single response variables against multiple abiotic factors: Shannon's species diversity, species richness, species evenness, Simpson's species dominance, individual tree size inequality, functional divergence, functional dominance and aboveground biomass (Pielou, 1969; Shannon, 1948; Simpson, 1949). The species' relative basal area was used to weight the number of tree species for the calculations of Shannon's species diversity, evenness and Simpson's dominance within each plot, as suggested by previous studies (Ali and Yan, 2017; Prado-Junior et al., 2016).

We used tree maximum height as a key plant functional trait for the calculations of functional dominance and divergence, which may substantially influence aboveground biomass (Ali et al., 2017; Conti and Díaz, 2013). Functional dominance (Eq. (1)) was calculated as the average tree maximum height values in each plot, weighted by the species' relative basal area, which represents the expected variety of a single trait values within a given plot (Díaz et al., 2007). Functional divergence (Eq. (2)) was quantified as the variance in tree maximum height values weighted by the species' relative basal area in each plot (Mason et al., 2003).

$$CWM_x = \sum_{i=1}^{s} p_i t_i \quad (1)$$

$$FDvar = 2/\pi \arctan(5V) \text{and } V = \sum_{i=1}^{s} p_i (\ln x_i - \ln x)^2 \quad (2)$$

where CWM_x is the CWM for trait x, $FDvar_x$ is the functional divergence of trait x, s is the number of species in the plot, p_i is the relative basal area of ith species in the plot $p_i = a_i / \sum_{n=1}^{s} a_i$, and $\ln x = \sum_{i=1}^{s} p_i \ln x_i$. FDvar values range between 0 and 1 (Ali et al., 2017).

The coefficient of variation (a measure of relative variability) of tree height, the ratio of the standard deviation of all tree height measurements to the mean tree height (Eq. (3)), was used to quantify the individual tree size inequality within each plot, expressed as a percentage (Ali and Mattsson, 2017; Ali and Yan, 2017). We used the relative variability of individual trees heights, because the individual tree size inequality represents the niche complementarity and facilitation effects (Yachi and Loreau, 2007).

$$CV_j = \frac{s_j}{\overline{x}_j} \times 100 \quad (3)$$

where CV_j is the individual tree size variation, s_j is the standard deviation of all tree heights measurements within jth plot, i.e. $s_j = \sqrt{\frac{\sum (x_j - \overline{x}_j)^2}{n_i - 1}}$, $\overline{x}_j$ is the mean tree height of the jth plot, i.e. $\overline{x}_j = \frac{\sum_{i=1}^{n} x_i}{n_i}$, and x_j is the value of each individual tree height in the jth plot being averaged. All the above biotic attributes were quantified or calculated using the *vegan*, *FD*, *dbFD*, *functcomp* and *raster* packages.

We used the best-fit biomass allometric model for topical trees (Chave et al., 2014) for the quantification of aboveground biomass (Eq. (4)), and after that, the aboveground biomass of all individual trees was scaled up to the plot-level by converting into mega-gram per hectare. This global allometric model is based on tree DBH, height (H) and species' wood density (ρ), and has been widely applied for the estimation of aboveground biomass across (sub-) tropical forests of the world (Ali and Yan, 2017; Jucker et al., 2018; Poorter et al., 2017). Here, we collected wood densities of the species in the wood density databases (Chave et al., 2009; Reyes et al., 1992; Zanne et al., 2009). In those cases, wood densities of specific-species were not found, genus- or family- or plot-level mean wood density values were used instead, as suggested by several previous critical studies (e.g. Jucker et al., 2018).

$$AGB = 0.0673 \times \left(\rho \times DBH^2 \times H\right)^{0.976} \quad (4)$$

The summary of biotic variables used in the analysis is listed in Table S1.

2.3. Explanatory variables: Abiotic drivers

In this study, we used nine abiotic factors for explaining variation in each of the above mentioned biotic factors: elevation, climatic water

availability, mean annual temperature, soil fertility, soil textual properties (sand, silt and clay), gravel and soil pH.

We first recorded the geographical coordinates (latitude and longitude) and elevation of each plot using a handheld Geographic Positioning System. We then extracted mean annual temperature, mean annual temperature and mean annual potential evapotranspiration for each plot from a global climate dataset (http://www.worldclim.org/). We calculated climatic moisture index, through the subtraction of mean annual potential evapotranspiration from mean annual precipitation, to represent the climatic water availability. Higher values of climatic moisture index represent higher water availability for plants (Hogg, 1997).

We obtained soil total exchangeable bases (soil TEB; the sum of base cations Ca^{2+}, Mg^{2+}, K^{+} and Na^{+}, in cmol kg^{-1}), soil textural fractions (i.e., sand, silt and clay, in %wt.), gravel content (in %vol.), and soil pH ($-\log(H^{+})$) of the topsoil (0–30 cm) and subsoil (30–100 cm) from the Harmonized World Soil Database (FAO et al., 2012). We used a mean value for each of these soil physicochemical properties of the topsoil and subsoil for each plot to better represent the edaphic factors for biotic attributes (Poorter et al., 2017). We acknowledge that soil phosphorus, nitrogen and other nutrients are also important for determining the biotic attributes, but unfortunately, these data were not available in the Harmonized World Soil Database. The summary of abiotic variables used in the analysis is listed in Table S1.

2.4. Statistical analyses

We used boosted regression trees (BRT) models to examine how each biotic attribute is driven by multiple abiotic drivers, including climatic water availability, mean annual temperature and edaphic factors, across large-scale elevation gradients in tropical forests. Here, we included elevation as a covariate to account for the interactions of elevation with abiotic factors as well its influence on a given tested biotic attribute. The BRT approach is rooted in advancements in machine learning algorithms, where the final best model is “learned” from the data and not predetermined. Because of reducing bias and maximizing explained variance, the BRT approach may be better-appropriate to test the relative contributions of multiple abiotic factors for biotic attributes in natural forests (Yuan et al., 2018). Boosting, or more specifically, stochastic gradient boosting, increases explanatory power by reducing the over-learning, or overfitting, that usually occurs with simple regression trees. Because of these advantages of the BRT method over other statistical models (De'ath, 2007; Elith et al., 2008), there has been recent motivation in tree-based models for ecological applications particularly for assessing the relationships between abiotic and biotic factors in natural forests (Lin et al., 2016; Yuan et al., 2018).

We fitted 4 BRT models for each biotic attribute with a combination of the following recommended settings for ecological modelling (De'ath, 2007; Elith et al., 2008): learning rate of 0.001, bag fractions of 0.60, and a tree complexity of 1, 2, 3 and 4 to account for potential higher order interactions. The above model-testing technique was repeated 49 times for each model because BRT outputs from cross-validation can largely differ due to the bag fraction depending on the random selection of points for the folds. So, the average of 49 repeated models was used for the model fit statistics and validations. We selected to show our results based on the recommended best learning rate (0.001) for ecological modelling, less prediction error (i.e. % changes in prediction error) and low tree complexity for the purpose to avoid over-learning (Table S2). A Gaussian distribution was used for all BRT models because most of the biotic attributes comprise continuous numerical variables. However, some of the biotic attributes (e.g. species richness, individual tree size variation, functional dominance and aboveground biomass) were natural-logarithm transformed and standardized, to obtain a mean of 0 and a standard deviation of 1, to improve normality, comparison among multiple predictors, and to reduce the model error (Yuan et al., 2018).

The percentages of variation by multiple abiotic factors represent their relative contributions to total variation (i.e., R^2) explained by the BRT model for a given response variable (i.e. biotic attribute). The importance of each abiotic factor was assessed based on both the relative contribution to the explained variation and the modelled relationship for a given abiotic factor versus biotic attribute. All BRT analyses were carried out in R 3.4.2 using the *gbm* and *caret* packages and other complementary functions (De'ath, 2007; Elith et al., 2008). The histograms of the studied biotic and abiotic variables including tree DBH and height of all individuals are provided in Fig. S2. The matrix of Pearson's correlation for each pair of the test variables is provided in Fig. S3.

3. Results

The tested multiple abiotic factors (i.e. elevation, climatic water availability, mean annual temperature, soil pH, gravel, sand, silt, clay and soil fertility) explained simultaneously 43, 50, 36, 45, 37, 50, 17 and 46%, respectively, of the variations in Shannon's species diversity, species richness, species evenness, Simpson's dominance, individual tree size variation, functional dominance, functional divergence and aboveground biomass (Table 1). Although the relative contributions of abiotic factors to biotic attributes were different across large-scale elevational gradients, climatic water availability accounted for most (i.e. 15.52 to 25.30%) of the variations in all biotic attributes after the large influences of elevation (i.e. 30.43 to 62.83%). Soil fertility explained 0.36 to 17.68% of the variations in biotic attributes, followed by silt content (2.44 to 14.21%), soil pH (2.79 to 9.61%), mean annual temperature (1.76 to 8.39%), gravel (1.92 to 7.03%), clay (1.65 to 3.38%), and sand (0.61 to 2.08%) (Table 1).

Taxonomic diversity-related biotic attributes (i.e. Shannon's diversity, species richness, evenness and Simpson's dominance) increased with increasing climatic water availability while showing generally increasing to slight humpbacked type relationships with elevational

Table 1
Results of boosted regression tree analysis (BRT) of biotic attributes versus abiotic factors in tropical forests. ‘Abiotic drivers' relative importance’ shows the relative contributions (in %) or influences of multiple abiotic factors to the accounted variation of each BRT model for biotic factors in tropical forests.

BRT models for biotic attributes	Abiotic drivers' relative importance									Model statistics and validations			
	Elevation	CMI	MAT	pH	Gravel	Sand	Silt	Clay	Soil TEB	TC	PE	Trees	R^2
Hs	54.37	22.58	2.21	9.61	3.82	0.97	4.29	1.65	0.50	2	0.35	9500	0.43
ln (SR)	57.14	19.60	1.76	9.40	4.00	0.61	4.99	2.14	0.36	3	0.60	7450	0.50
SE	51.10	21.30	9. 20	4.97	2.03	2.80	4.48	2.65	1.47	2	0.01	7900	0.36
SD	62.83	15.52	8.39	4.09	1.92	1.99	2.44	2.34	0.47	2	0.01	6900	0.45
ln (CV H)	32.43	20.04	7.92	3.30	7.03	1.04	14.21	3.38	10.64	3	0.73	7000	0.37
ln (CWM Hmax)	53.20	17.78	6.60	4.66	3.12	0.79	4.87	2.59	6.39	3	0.60	7800	0.50
FDvar Hmax	30.43	25.30	3.43	2.79	2.14	2.51	13.09	2.63	17.68	2	0.01	4650	0.17
ln (AGB)	53.21	17.12	7.67	6.77	2.78	1.61	4.30	2.80	3.73	3	0.66	7750	0.46

Abbreviations: Hs, Shannon's species diversity; SR, species richness; SE, species evenness; SD, Simpson's species dominance; CV H, coefficient of variation of tree heights (individual tree size variation); CWM Hmax, functional dominance; FDvar Hmax, functional divergence; AGB, aboveground biomass; *ln*, natural-logarithm; CMI, climatic moisture index (i.e. climatic water availability); MAT, mean annual temperature (i.e. heat); pH, soil pH; Soil TEB, soil total exchangeable bases (soil fertility); TC, tree complexity; PE, prediction error; Trees, n.trees (BRT model index); R^2, coefficient of determination.

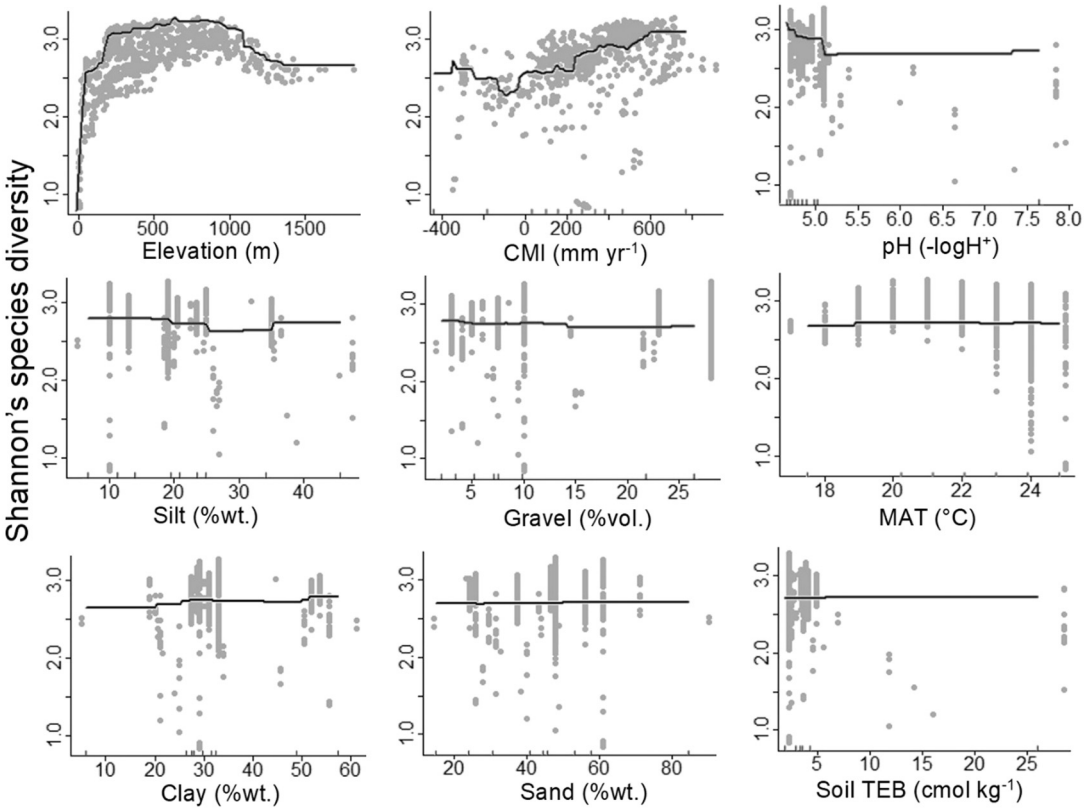

Fig. 1. Modelled relationships (solid lines) between Shannon's species diversity and multiple abiotic factors including elevation, climatic water availability (i.e. climatic moisture index; CMI), mean annual temperature (MAT; i.e. heat), soil total exchangeable bases (soil TEB; i.e. soil fertility), soil pH, soil textural properties (sand, silt and clay contents) and gravel contents across 907 tropical forest plots. Background points show the observed values for the 907 forest plots.

gradients (Figs. 1, 2, 3 & 4). Tree size or biomass-related biotic attributes (i.e. individual tree size inequality, aboveground biomass, functional dominance and divergence) showed unclear trends with climatic water availability while showing generally increasing trends with elevational gradients (Figs. 5, 6, 7 & 8). More specifically, individual tree size variation and functional dominance showed strong decreasing and increasing trends with climatic water availability (Figs. 5 & 6). Functional divergence showed a generally decreasing trend with climatic water availability (Fig. 7). Aboveground biomass decreased with low climatic water availability and then plateaued with slight decreasing trend after small peaking with high climatic water availability (Fig. 8).

Tree size or biomass-related attributes decreased with increasing mean annual temperature and soil pH, but monotonically increased with soil fertility, from 0 to 8 cmol kg^{-1}, and then plateaued with soil fertility >8 cmol kg^{-1} (Figs. 5, 6, 7 & 8). By contrary, taxonomic diversity-related attributes were weakly related with mean annual temperature and soil fertility, but monotonically decreased with soil pH, from 5 to 5.2, and then plateaued with soil pH > 5.2 having very slight increasing or decreasing trends (Figs. 1, 2, 3 & 4). Soil textural properties and gravel content did not show any apparent relationships with taxonomic diversity-related attributes (Figs. 1, 2, 3 & 4), but show weak to moderate increasing or decreasing relationships with tree size or biomass-related attributes (Figs. 5, 6, 7 & 8). More specifically, functional divergence increased with silt content, from 17 to 27%wt., but decreased monotonically at high clay content (i.e. 55%wt.), and then plateaued. As such, individual tree size variation and functional dominance increased monotonically with silt and gravel contents but decreased with clay content. Aboveground biomass increased monotonically with gravel content from low to high, whereas also increased with silt content <25%wt., and then decreased markedly with no further clear change with silt content >27%wt.

4. Discussion

In this study, we evaluated the relative contributions of the multiple abiotic drivers for multiple biotic attributes in tropical forests by using a BRT modelling framework. We found that, after elevation, climatic water availability is the main determining factor for all studied biotic attributes in the studied tropical forests. In addition, we also found that most of the studied biotic attributes decreased apparently with mean annual temperature but increased with soil fertility whereas the soil textural properties had negligible influences.

In line with our hypothesis, we found that, after the large influences of elevation (i.e. explained 49.34% of the variation, at average) as a covariate, climatic water availability is the most important abiotic factor (i.e. 19.91%) than temperature (i.e. 5.43%) and edaphic factors (i.e. <7%) in affecting the multiple biotic attributes in tropical forests. Despite the increasing trend along large-scale elevational gradients, results in this study indicate that taxonomic diversity-related biotic attributes are positively related to climatic water availability but negligibly related to mean annual temperature. In addition, climatic water availability increased but mean annual temperature decreased with elevation in the studied forests (Fig. S3), which may largely explain the high contribution of climatic water availability relative to temperature for species diversity across large-scale elevational gradients (Bhattarai and Vetaas, 2003; Kluge et al., 2006). For example, our studied tropical forests are at the low- to mid-range of the precipitation gradient (i.e.1008–2038-mm $year^{-1}$), and climatic water availability is, therefore, a main limiting factor as compared to the forests at higher range of the precipitation gradient, where nutrient and energy availabilities might be the limiting factors (Lohbeck et al., 2013; Toledo et al., 2012). As such, the strong relationship of species distribution with climatic water availability has been reported in numerous studies (Bongers et al., 1999; Borchert,

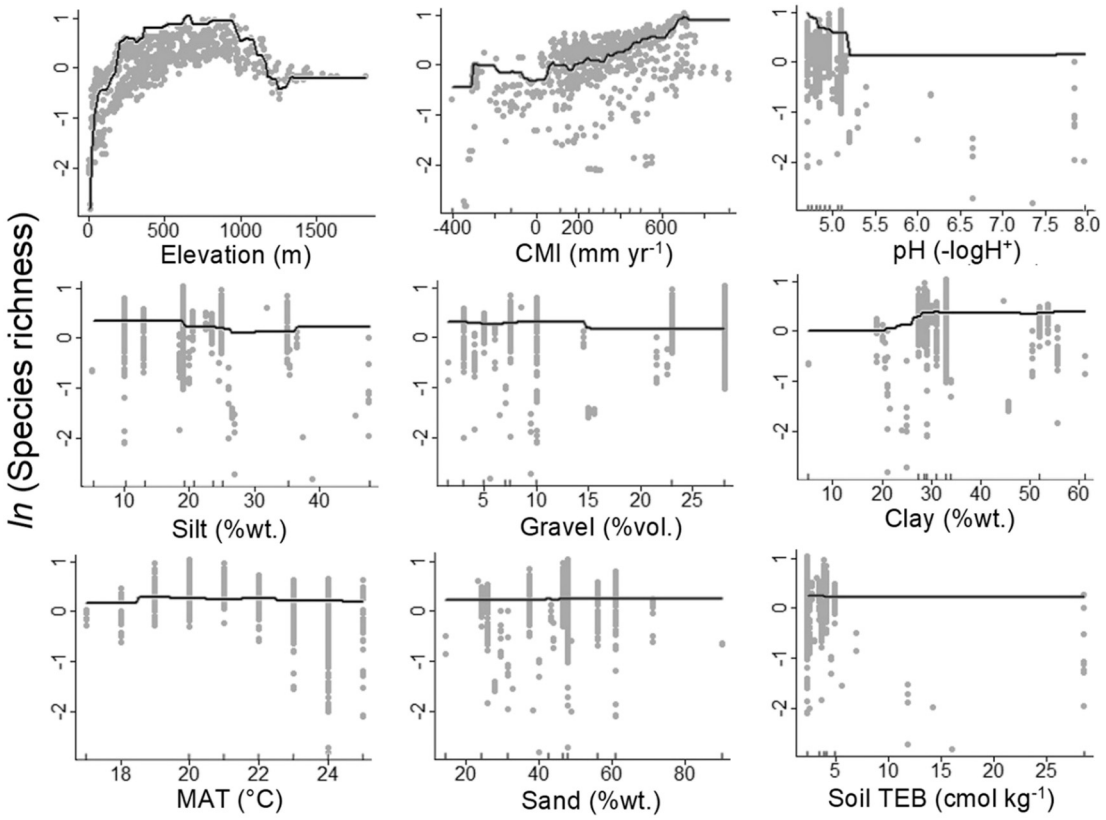

Fig. 2. Modelled relationships (solid lines) between the natural logarithm of species richness and multiple abiotic factors. The multiple abiotic factors are elevation, climatic water index (CMI, i.e. climatic water availability), mean annual temperature (MAT; i.e. heat), soil total exchangeable bases (soil TEB; i.e. soil fertility), soil pH, soil textural properties (sand, silt and clay contents) and gravel contents. Background points show the observed values for the 907 forest plots.

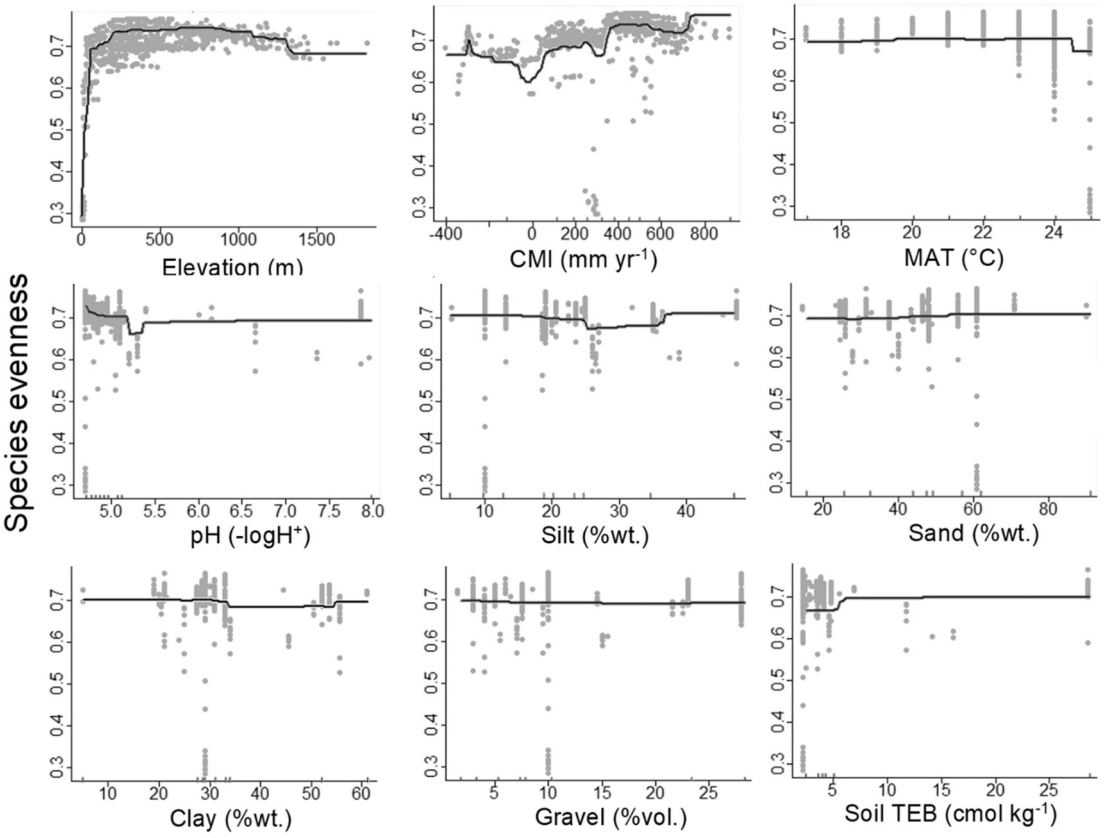

Fig. 3. Modelled relationships (solid lines) between species evenness and multiple abiotic factors. General explanation and the meaning of all acronyms are provided in the caption of Fig. 2.

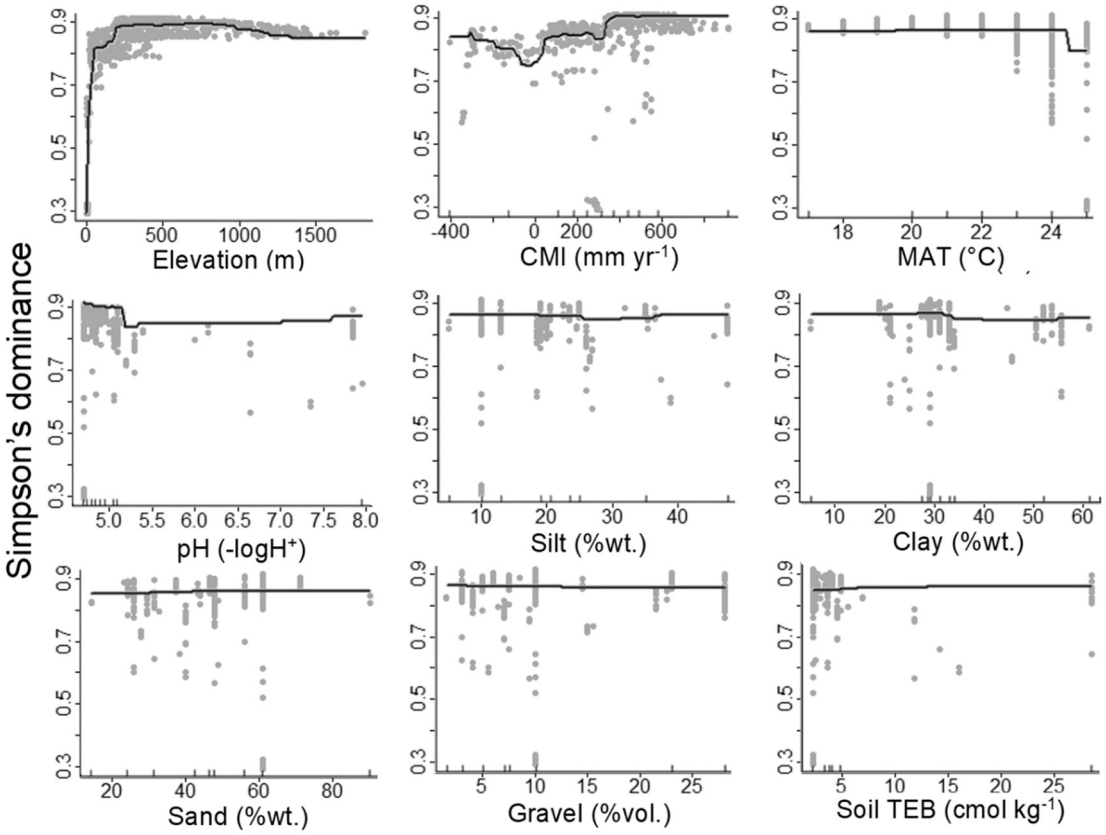

Fig. 4. Modelled relationships (solid lines) between Simpson's dominance and multiple abiotic factors. General explanation and the meaning of all acronyms are provided in the caption of Fig. 2.

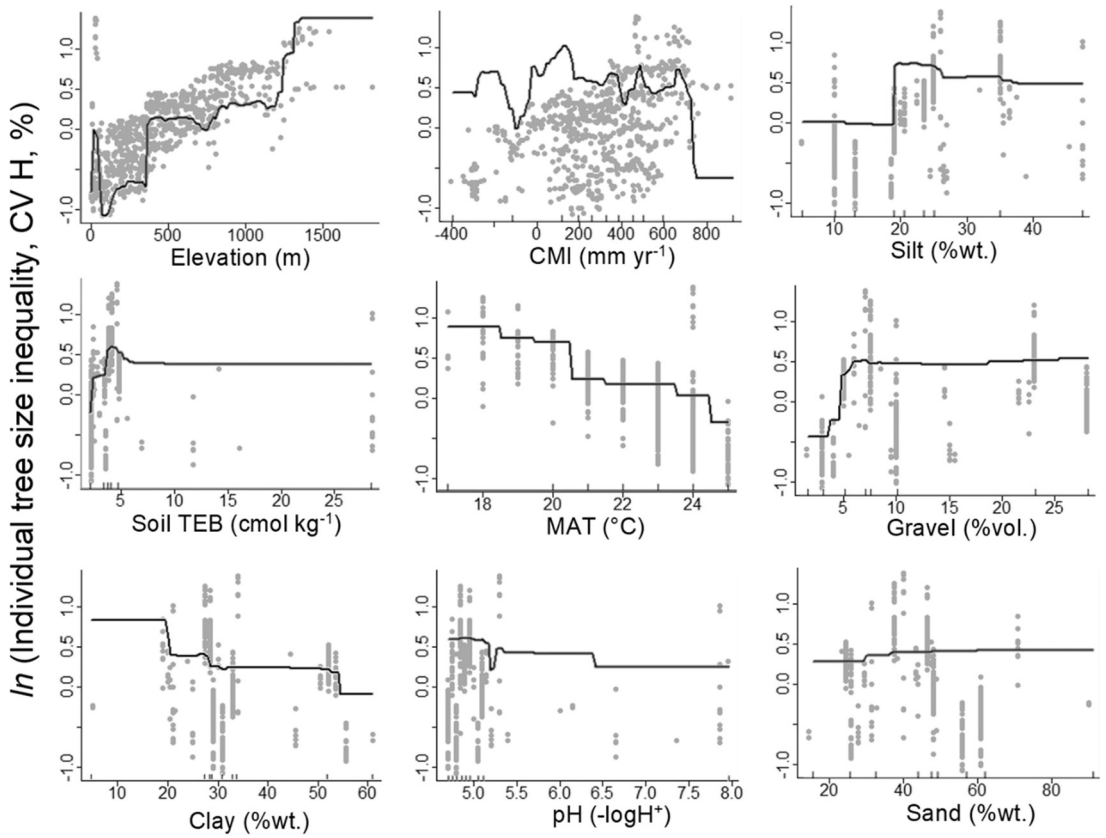

Fig. 5. Modelled relationships (solid lines) between the natural logarithm of individual tree size variation and multiple abiotic factors. General explanation and the meaning of all acronyms are provided in the caption of Fig. 2.

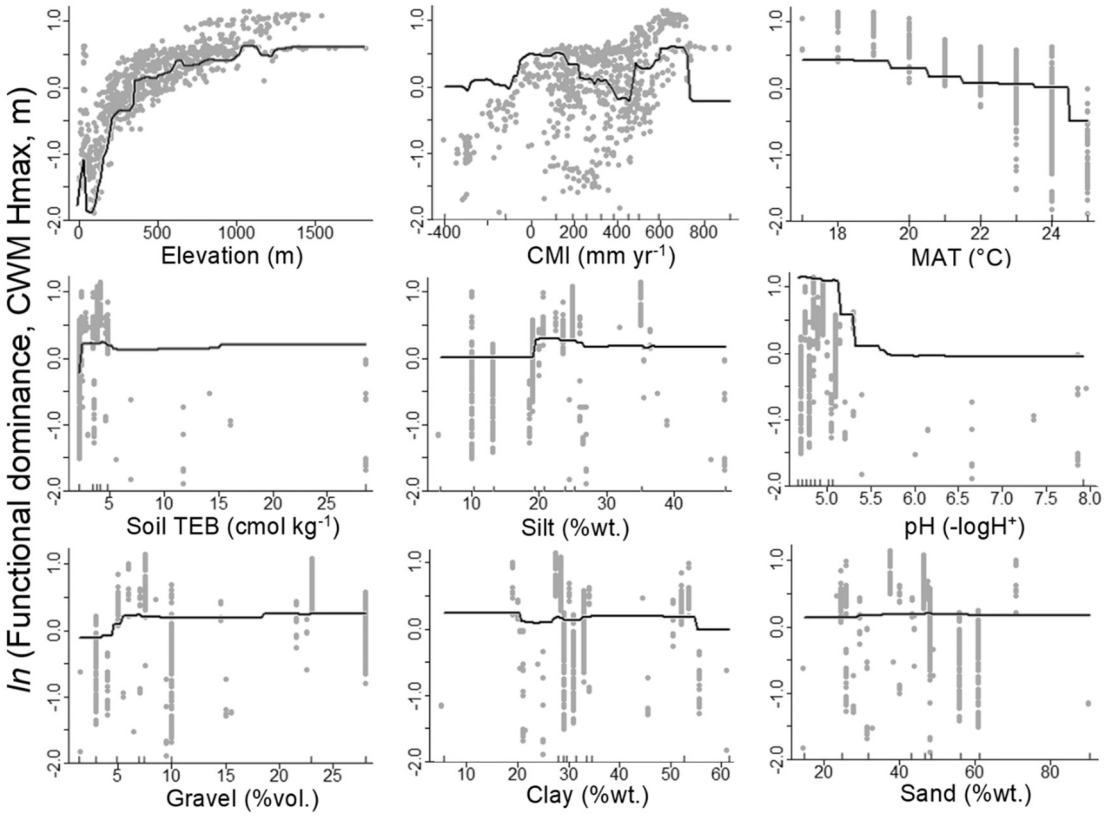

Fig. 6. Modelled relationships (solid lines) between the natural logarithm of functional dominance and multiple abiotic factors. General explanation and the meaning of all acronyms are provided in the caption of Fig. 2.

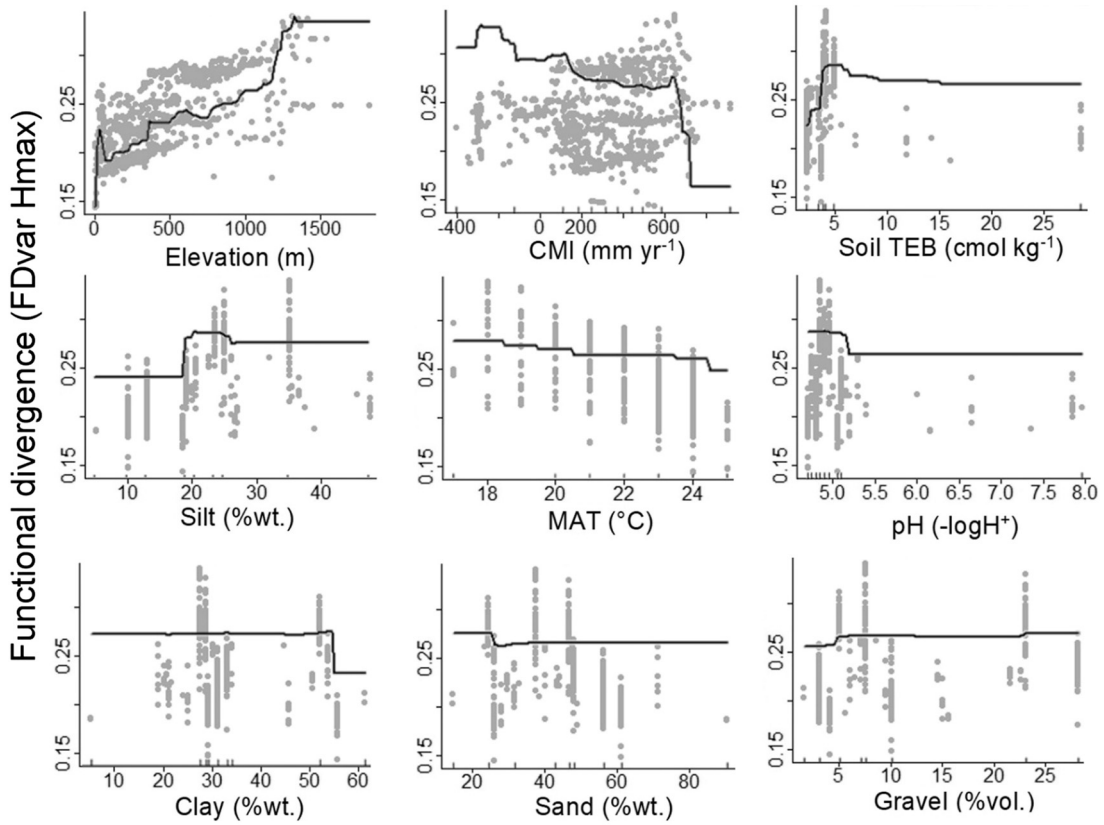

Fig. 7. Modelled relationships (solid lines) between functional divergence and multiple abiotic factors. General explanation and the meaning of all acronyms are provided in the caption of Fig. 2.

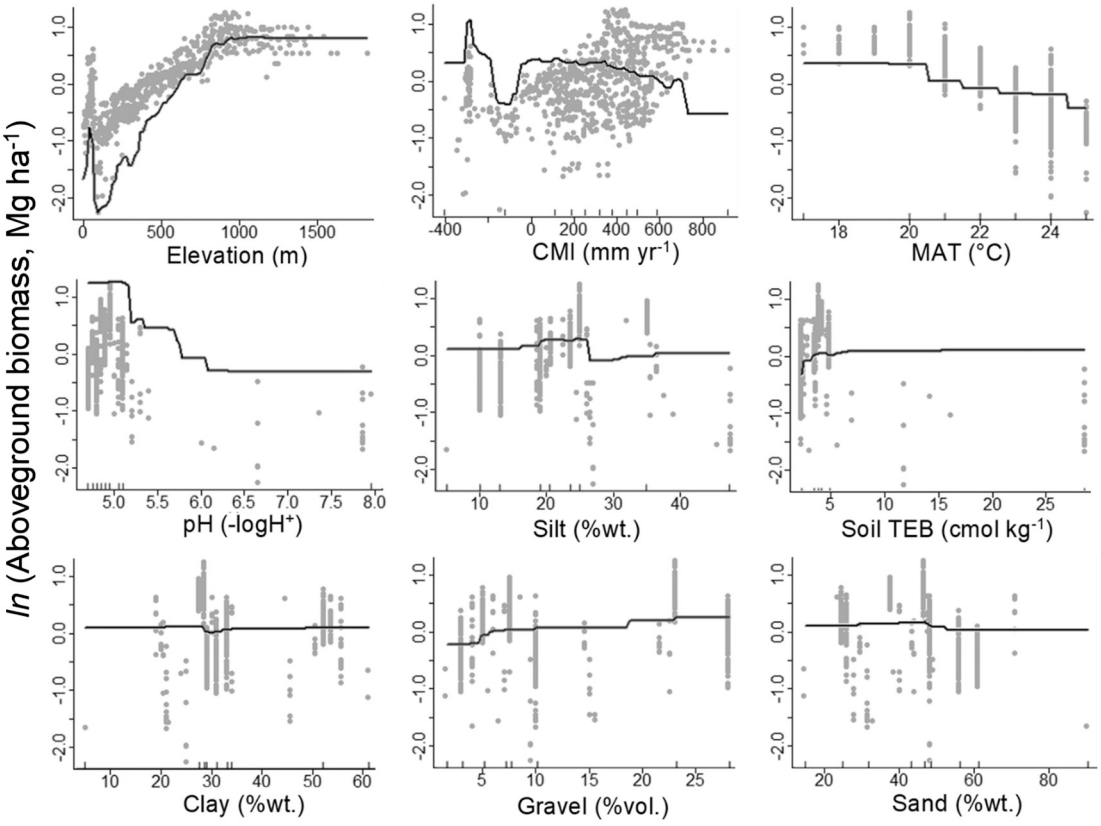

Fig. 8. Modelled relationships (solid lines) between the natural logarithm of aboveground biomass and multiple abiotic factors. General explanation and the meaning of all acronyms are provided in the caption of Fig. 2.

1998; Engelbrecht et al., 2007; Toledo et al., 2012), and hence it is reasonable that climatic water availability is a key limiting factor of biotic factors in tropical forests (Poorter et al., 2017).

Experimental and natural studies have suggested that seasonal drought relative to other factors (e.g. temperature and soil nutrients) may have a stronger influence on the tree growth, recruitment and survival because it can directly affect the plant metabolic rates and physiology in the short term (Engelbrecht et al., 2005; Michaletz et al., 2014; Phillips et al., 2010; Poorter and Markesteijn, 2008). Therefore, it is reasonable that climatic water availability indeed increases biomass-related variables such as biomass growth of survivor and biomass stocks (Poorter et al., 2017), probably due to the longer length of the growing season related to the high precipitation over the year (Toledo et al., 2012). However, in this study, individual tree size variation and functional dominance showed strong decreasing and increasing trends while functional divergence showed a generally decreasing trend with climatic water availability. Whereas, aboveground biomass decreased at the lower edge of the climatic water availability and then plateaued with slight decreasing trend after small peaking with high climatic water availability. These conflicting unclear results as compared to the taxonomic diversity-related biotic attributes might be attributable to the fact that climatic water availability limits the ability of plants to utilize available energy (either solar radiation or temperature) (Evans et al., 2005). As such, we also found that these tree size or biomass-related biotic attributes as compared to the taxonomic diversity decreased apparently with increasing mean annual temperature while showing unclear trends with climatic water availability, which might be attributable to the influence of seasonal drought across large-scale elevational gradients (Ciais et al., 2005). In sum, climatic water availability is, therefore, an important limiting factor of the species diversity as well as productivity-related biotic attributes in tropical forests across large-scale elevational gradients (Poorter et al., 2017; Toledo et al., 2012). This study suggests that tree size or biomass-related biotic attributes are sensitive to drought and heat whereas the taxonomic diversity-related biotic attributes make the studied tropical forest more resilient to climate change across large-scale elevational gradients (Poorter et al., 2017; Toledo et al., 2012).

One of the important findings of this study is that mean annual temperature had negligible influences on taxonomic diversity-related biotic attributes, whereas tree size or biomass-related biotic attributes decreased apparently with mean annual temperature but the relative influence was relatively weak as compared to climatic water availability. Indeed, species richness is strongly temperature-dependent across large-scale geographical gradients, and hence increases exponentially with increasing environmental temperature within the favorable ranges (i.e. available energy) until the critical value of temperature (i.e. heat) (Berry and Bjorkman, 1980; Michaletz et al., 2014; Wright, 1983). The negligible influences of temperature relative to climatic water availability on taxonomic diversity might be attributable to the fact that climatic water availability limits available energy for plants (Evans et al., 2005). However, our results and those from previous studies highlight the importance of water–energy balance for influencing the tree size or biomass-related variables directly and indirectly via physiological responses of the species (i.e. taxonomic-related variables) (Chu et al., 2016; Michaletz et al., 2018). Therefore, the observed decreasing pattern of tree size or biomass-related variables with mean annual temperature might be related to the fact that heat can influence species diversity and productivity indirectly via plant size or biomass (Ciais et al., 2005; Michaletz et al., 2014). For example, it is theoretically plausible that rates of photosynthesis and respiration increase exponentially with temperature (i.e. the use of available energy) to a critical level of temperature (i.e. high temperature, and hence heat) beyond which rates decrease across large-scale or relevant temperatures (Berry and Bjorkman, 1980; Michaletz et al., 2014). However, it is also plausible

that photosynthetic rate and hence aboveground biomass increase with climatic water availability (Huxman et al., 2004; Ponce-Campos et al., 2013; Poorter et al., 2017). These contrasting patterns suggest that climatic variables (i.e. water and temperature) influence tree size or biomass-related variables directly via metabolic kinetics (Chu et al., 2016). Furthermore, local adaptation of thermal and edaphic tolerances may restrict the physiological responses of the species (i.e. taxonomic-related variables) (Enquist et al., 2007; Kerkhoff et al., 2005), and hence climate influences may result not directly from changes in metabolic rates but rather indirectly via individual tree size variation, aboveground biomass, stand structure and age, and growing season length (Michaletz et al., 2018). Therefore, efforts to predict biotic attributes in response to climatic change should include the mechanisms that govern maximum plant size or biomass-related variables (Michaletz et al., 2014).

In this study, we also found that edaphic factors relative to climatic factors had explained very less or a negligible amount of the variations in most of the studied biotic attributes in tropical forests. Numerous explanations might elucidate the lower contribution of edaphic factors relative to the climate in our and other tropical forests (Poorter et al., 2017; Toledo et al., 2012). For example, climate acts a fundamental ecological filter at larger geographical scales, whereas edaphic factors act as a supplementary filter under similar environmental conditions at smaller local scales (Swaine, 1996). As such, we found that climatic factors relative to edaphic factors had strong correlations with elevation (Fig. S3) and that elevation had accounted for most of the variations in biotic factors, thereby indicating that climatic water availability is the main limiting factor of biotic factors across large-scale elevational gradients in the studied forests. More specifically, soil fertility (i.e. the soil total exchangeable bases) and soil pH explained only 5.16% and 5.70% (at average) of the variations in most of the studied biotic factors, respectively. Indeed, edaphic factors are influencing biotic factors in climatically homogeneous environments at small local scales (Ali and Yan, 2017; Clark et al., 1998; Harms et al., 2001). As such, we found that biotic attributes monotonically increased with soil fertility but decreased with soil pH at lower edge (i.e. acidic), although the relative contributions were less in most cases. In addition, we also found that soil textural properties and gravel contents explained <7% (at average) of the variations in biotic attributes. Soil texture may greatly influence the soil water-holding capacity and hence may strongly alter the availability of soil water to plants, which may, in turn, influence the species diversity (Sanaei et al., 2018; ter Steege et al., 1993). As such, we found that most of the biotic attributes are slightly apparently related to the gravel, clay and silt contents suggesting that studied tropical forest species prefer edaphically wet soils. This result applies the importance of soil water availability as a determinant of biotic attributes (Aubry-Kientz et al., 2015; Toledo et al., 2012), and we hope that our study will encourage further studies on this point, i.e. the relative contribution of climatic and soil water availability for biotic attributes.

Lastly, we acknowledge that elevation is a key spatial driver of both taxonomic-related and tree size or biomass-related biotic attributes in the studied tropical forests, as it explains a large amount of variations in the studied biotic attributes. However, it is well-understood that elevation determines climate and soil for driving biotic factors and ecosystem functioning (Jucker et al., 2018). Therefore, in this study, we used elevation as a covariate with climate and edaphic factors for predicting biotic attributes, in order to control the large influence of elevation because climate and edaphic factors are the spatial drivers of biotic attributes in tropical forests (Poorter et al., 2017; Toledo et al., 2012). However, further understandings are necessary to evaluate how climatic, edaphic and biotic factors simultaneously influence ecosystem functioning (Michaletz et al., 2018; Poorter et al., 2017), while accounting for the direct and indirect effects of spatial factors (e.g. longitude, latitude and elevation) on them (Jucker et al., 2018), in the structural equation modelling, which can be more informative in understanding macroecological mechanisms or biogeographical patterns.

5. Conclusions

This study strongly reveals that climatic water availability is the main determining factor for all studied biotic attributes in the studied tropical forests across large-scale elevational gradients. Tree size or biomass-related rather than taxonomic-related biotic attributes also decrease apparently with mean annual temperature. Future climate change (i.e. a decrease in climatic water availability with an increase in mean annual temperature) is thus likely to have a substantial influence on the biotic attributes in the tropical forests. This study suggests that efforts to predict biotic attributes in response to climatic change should include the tree size or biomass-related variables in complex natural forests. This study concludes that biotic attributes are very sensitive to future drought (i.e. low climatic water availability) and heat (i.e. high temperature beyond the critical value) in the studied tropical forests across large-scale elevational gradients.

Data availability

A summary of the studied species is provided in Appendix A. A summary of the variables used in this study is provided in Table S1 (Appendix B). More information about the dataset is available upon reasonable request to the authors.

Contribution of the co-authors

AA and HSJ designed the study. SLL, JKH, FMK, JHY and HSJ collected field data. AA complied and analyzed the data and wrote the manuscript. SLL, JKH and HSJ contributed critically to the draft. All coauthors gave final approval for publication. The authors declare that they have no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2018.08.072.

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